



Cannibalism of young is related to low paternity and nest take-overs in an intertidal fish

Aneesh P. H. Bose^{a, *}, Malcolm J. Lau^b, Karen M. Cogliati^{a, 1}, Bryan Neff^b, Sigal Balshine^a

^a Aquatic Behavioural Ecology Laboratory, Department of Psychology, Neuroscience, & Behaviour, McMaster University, Hamilton, ON, Canada

^b Department of Biology, Western University, London, ON, Canada

ARTICLE INFO

Article history:

Received 15 December 2018

Initial acceptance 21 January 2019

Final acceptance 2 April 2019

MS. number: A18-00893R

Keywords:

cuckoldry
filial cannibalism
infanticide
male competition
microsatellite genotyping
parental care
toadfish

Parental care is costly, and theory suggests that caregivers should reduce parental investment or even stop caring altogether when the costs of caring are too high or the benefits too low. Brood cannibalism is one tactic by which parents can divert investment away from current offspring and towards potentially higher-quality future offspring, but the various selective factors underlying partial brood cannibalism and their relative importance remain poorly understood. Here we used the plainfin midshipman fish, *Porichthys notatus*, to concurrently examine three hypotheses for partial brood cannibalism and test whether cannibalism increases when (1) parental body condition is low, (2) brood sizes are large and/or (3) brood paternity is low. To investigate these predictions, we combine multiyear, multisite field data with genetic paternity testing and show that partial brood cannibalism is not related to low parental body condition or to large brood sizes, but rather is linked to low paternity. In particular, males that had taken over nests from other males, and were thus unrelated to the broods present in the new nests, consumed the largest number of young (~15 or more eaten at a time). Our data also suggest that the consumption of only a few young (~1–2 at a time) appears to be governed by other factors that are not clearly related to paternity. Overall, we highlight the utility of concurrently testing multiple hypotheses for partial brood cannibalism within the same system to better understand this otherwise puzzling behaviour.

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Parental care and offspring cannibalism frequently co-occur. These apparently opposing behaviours are linked in a surprisingly large number of species and across a wide range of phylogenetically distinct taxa (Elgar & Crespi, 1992; Manica, 2002; Polis, 1981). While parental care promotes the survival and development of young (Smiseth, Kolliker, & Royle, 2012), cannibalism results in their termination. Thus, these two behaviours often appear to work in opposition to one another. Yet cannibalizing some or all offspring is thought to be adaptive for parents under some circumstances (Elgar & Crespi, 1992; Klug & Bonsall, 2007; Manica, 2002; Payne, Smith, & Campbell, 2004). While complete brood cannibalism (when all the young are eaten) is considered to be an investment into future reproduction, partial brood cannibalism is viewed as an investment into future reproduction and/or into the remaining current offspring (Rohwer, 1978; Sargent, 1992).

The phenomenon of ending care by complete brood cannibalism has been well studied in fishes and it is more common when broods are small, as seen in fathead minnows, *Pimephales promelas* (Sargent, 1988), damselfishes, *Stegastes dorsopunicans* and *Microspathodon chrysurus* (Peterson, 1990), fantail darters, *Etheostoma flabellar* (Lindström & Sargent, 1997), and bluegill sunfish, *Lepomis macrochirus* (Neff, 2003). Full broods may also be more readily cannibalized by caregivers when alternative mating opportunities are abundant and the broods can be replaced quickly (Deal & Wong, 2016), as has been suggested for cardinal fish (*Apogon doederleini*, *Apogon niger*; Okuda, 1999; Okuda & Yanagisawa, 1996). In addition, two studies on threespine stickleback, *Gasterosteus aculeatus*, have shown that caring males are more likely to completely cannibalize broods under conditions of low paternity, which typically arises as a result of cuckoldry (Frommen, Brendler, & Bakker, 2007; Mehlis, Bakker, Engqvist, & Frommen, 2010). Because parental care also imposes costs to caregivers (Trivers, 1972), complete brood cannibalism can be thought of as a form of infanticide that occurs when the reproductive benefits of the current offspring are too low relative to the costs parents would have to pay to raise them (Clutton-Brock, 1991; Manica, 2002).

* Correspondence: A. P. H. Bose, Max Planck Institute for Ornithology, Department of Collective Behaviour, Universitätsstr. 10, 78464, Konstanz, Germany.

E-mail address: aphbose@gmail.com (A. P. H. Bose).

¹ K. M. Cogliati is now at the Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, U.S.A.

In contrast to our knowledge of the drivers of complete brood cannibalism, we still have a relatively poor understanding of the factors that underlie partial brood cannibalism. Numerous non-mutually exclusive hypotheses have been proposed for partial brood cannibalism but few studies have comprehensively explored more than one of these hypotheses concurrently. First, the 'energy reserves hypothesis' proposes that caregivers may cannibalize a portion of their offspring to acquire energy needed to continue to provide care or to offset the costs of care (Rohwer, 1978; e.g. threespine sticklebacks, *G. aculeatus*; ; Mehlis, Bakker, & Frommen, 2009; bluegill sunfish, *L. macrochirus*; ; Neff, 2003; assassin bugs, *Rhinocoris tristis*; ; Thomas & Manica, 2003; maritime earwigs, *Anisolabis maritima*; ; Miller & Zink, 2012). Second, the 'density dependence hypothesis' states that when offspring survival is density dependent, parents cannibalize some of their own offspring to prevent overcrowding, which might jeopardize the whole brood (Klug & Bonsall, 2007; e.g. burying beetles, *Nicrophorus vespilloides*; ; Bartlett, 1987; beaugregory damselfish, *Stegastes leucostictus*; ; Payne et al., 2004; sand gobies, *Pomatoschistus minutus*; , 2002; Lissåker, Kvarnemo, & Svensson, 2003). Third, the 'brood size hypothesis' states that large broods are more susceptible to partial brood cannibalism because the fitness cost of consuming individual young decreases proportionally with brood size (Hoelzer, 1995), although empirical support for this third relationship has been especially scarce (Manica, 2002). Fourth, the 'offspring quality hypothesis' posits that partial brood cannibalism is more likely if the quality of some offspring is low (Klug & Bonsall, 2007). For example, certain low-quality offspring may be more likely to be cannibalized if they are diseased (e.g. sphynx blennies, *Aidablennius sphynx*; Kraak, 1996) or if they have been parasitized (as occurs in the assassin bug, *R. tristis*, if their eggs are infected by scelionid wasps; Thomas & Manica, 2003). Fifth, the 'relatedness hypothesis' states that when parentage within and between broods is variable, a cannibalistic parent should preferentially consume nonkin young (Manica, 2002). This is not an exhaustive list of hypotheses for partial cannibalism, although, to date, other ideas have received far less research attention (e.g. Klug & Lindström, 2008; Sikkell, 1994; Vallon & Heubel, 2016). Recently, filial cannibalism has also been studied through the lens of consistent individual differences in behaviour, i.e. animal personality. In particular, individuals that are consistently more active may also display high levels of filial cannibalism, indicating that both activity and cannibalism can form a behavioural syndrome (Vallon, Grom, et al., 2016). Overall, empirical studies testing hypotheses and ideas about partial brood cannibalism have been either few and far between or largely equivocal, with support being found for some but not all hypotheses and support often only being found in some species and not others (Manica, 2002).

The question of how partial brood cannibalism is influenced by relatedness is particularly interesting because it is embedded within a broader, more heavily studied and debated research topic – that of the relationship between parental care and offspring parentage (Alonzo, 2010; Griffin, Alonzo, & Cornwallis, 2013; Kempnaers & Sheldon, 1997; Sheldon, 2002). To date, the relationship between partial brood cannibalism and parentage has yielded mixed results, although it has only been investigated in a handful of species. For example, in paternal caregiving fish species such as bluegill sunfish, *L. macrochirus* (Neff, 2003), scissortail sergeant, *Abudefduf sexfasciatus* (Manica, 2004), and *Telmatherina sarasinorum* (Gray et al., 2007), partial brood cannibalism increases when paternity (or certainty thereof) is low, but partial brood cannibalism does not correlate with paternity in sand goby, *P. minutus* (Svensson & Kvarnemo, 2007) or in the threespine stickleback, *G. aculeatus* (Mehlis et al., 2010). Cannibalistic adults may consume their own young or nonkin young, and they may do

so within their own nests or in the nests of other adults (e.g. neighbours, during 'raiding' events, as in the painted greenling, *Oxylebius pictus*; DeMartini, 1987). However, without the use of genetic tools, measuring the relative amounts of filial and nonkin cannibalism that occur in a system is a challenging undertaking (especially in the field), which is why few studies have attempted this. In light of the varied results regarding the link between cannibalism and relatedness, further empirical study of the relationship between partial brood cannibalism and parentage is warranted.

A powerful approach to studying partial brood cannibalism is to concurrently test several of the aforementioned, nonmutually exclusive hypotheses all within the same study system. Here, we concurrently test three hypotheses for partial brood cannibalism using a marine toadfish, the plainfin midshipman fish, *Porichthys notatus* (family Batrachoididae). In particular, we investigate how partial brood cannibalism relates to parental body condition (i.e. the energy reserves hypothesis), brood size (i.e. the brood size hypothesis) and offspring paternity (i.e. the relatedness hypothesis). The plainfin midshipman is a convenient species to test these hypotheses because males of this species provide sole parental care over a prolonged 3-month breeding season, which is an extremely energetically demanding task (Bose et al., 2014, 2015, 2016). Average brood size is ~560 young, although broods can range dramatically from fewer than 10 to over 3000 young per nest (Bose et al., 2018). Males also experience high variance in paternity between reproductive bouts (range 0–100% paternity/nest) and low overall paternity (mean \pm SE = 52 \pm 4%; Cogliati, Neff, & Balshine, 2013). This variance in paternity arises partially from aggressive nest take-overs (Bose et al., 2014; Cogliati et al., 2013) as well as from sperm competition with other males (Brantley & Bass, 1994; Cogliati et al., 2013; Fitzpatrick et al., 2015; Lee & Bass, 2004; Miller, Bose, Fitzpatrick, & Balshine, 2019). While the factors underlying offspring cannibalism in plainfin midshipman fish have previously been investigated in part (Bose et al., 2014, 2015), these past studies have primarily classified males into two discrete groups, 'recent cannibals' (i.e. males with young found in their digestive tracts) and 'noncannibals' (i.e. males with no young found in their digestive tracts). These studies did not focus on the number of young consumed by each male despite the valuable insights that this more detailed measure can provide. Cogliati et al. (2015) conducted paternity analyses on cannibalized young found within the digestive tracts of a small number ($N = 11$) of caregiving males, but they did not examine paternity of the other (nonconsumed) eggs in the males' broods for comparison. Here, we use data collected from wild fish sampled from multiple field sites across multiple years to build upon these previous studies and simultaneously test several hypotheses regarding partial brood cannibalism. We also explicitly test whether males engage in more offspring cannibalism when their paternity is low (i.e. examining the relatedness hypothesis). We do this by quantifying the genetic paternity of the young found in males' nests and the young that were cannibalized, i.e. found inside caregiving males' digestive tracts.

METHODS

Study Species

The plainfin midshipman fish is a marine toadfish distributed along the west coast of North America (Arora, 1948; Miller & Lea, 1972; Walker & Rosenblatt, 1988). During the breeding season (late April – early August), male fish vertically migrate from depths to the shallow intertidal zone and compete for large intertidal rocks under which they excavate nesting cavities (Fig. 1a). From these nests, males acoustically court females (Ibara, Penny, Ebeling, van

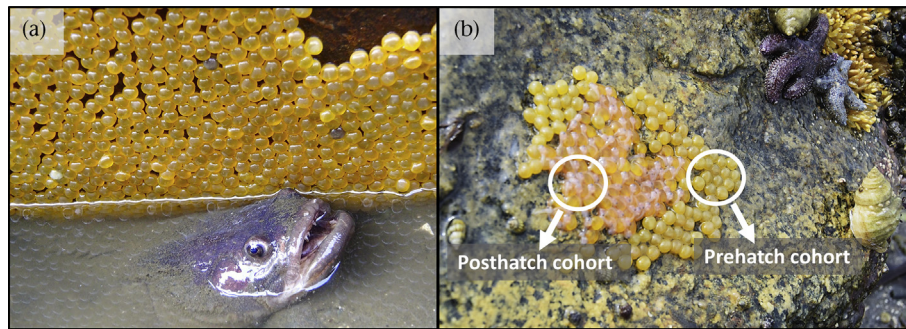


Figure 1. (a) Photograph of a guarder male in his intertidal nest with the rock overturned to show the young (eggs). (b) Photograph of a brood of young adhered to an overturned intertidal rock. This brood consists of two developmental cohorts, a younger prehatch cohort and an older posthatch cohort. Photo credit: Aneesh Bose.

Dykhuizen, & Cailliet, 1983), and once a female is attracted, she will lay her eggs in a monolayer on the roof of the nesting cavity (i.e. the underside of the intertidal rock; Arora, 1948; DeMartini, 1988). Males may attract multiple females to their nests over the course of the breeding season, and because young take ~60 days to become free-swimming and independent, this often leads males to simultaneously care for several temporally overlapping cohorts of young that differ in age (Fig. 1b). Young remain adhered to the rock surface via their yolk sac until they become free swimming. Because suitable nesting sites within the intertidal zone are limited (DeMartini, 1988), males compete vigorously for nest ownership, which often results in nest take-over events wherein one male is forcefully ousted by another who then acquires the nest and any young therein (Bose et al., 2014).

Male plainfin midshipman fish also engage in cuckolding behaviours via sneak or satellite spawning (Brantley & Bass, 1994; Lee & Bass, 2004). Adult males express one of two well-characterized alternative reproductive tactics (Bass, Horvath, & Brothers, 1996; Brantley & Bass, 1994; Cogliati, Balshine, & Neff, 2014; Lee & Bass, 2004). Type I, or conventional males, also called guarder males, are larger, fight for territories, build nests, court females and care for offspring, while Type II, or parasitic males, also called sneaker males, are smaller and they do not build or fight for nests, court females or care for offspring (Brantley & Bass, 1994). Both sneaker and guarder males can gain reproduction through cuckoldry (Cogliati, Balshine et al., 2014; Cogliati et al., 2013), but while sneaker males are obligate cuckolders, guarder males only cuckold when they have no offspring of their own (Brantley & Bass, 1994; Cogliati, Balshine et al., 2014; Lee & Bass, 2004).

Field Collections

In 2010, 2011, 2013 and 2015 between May and July, we located 347 plainfin midshipman guarder males and their nests in the intertidal zones of British Columbia, Canada (Ladysmith Inlet, Crescent Beach, Deep Bay, Mill Bay, Nanoose Bay) and California, U.S.A. (Tomales Bay). See Table 1 for sample sizes by field site and year and also see Cogliati, Mistakidis et al. (2014) and Bose et al. (2018) for more detailed information on each field site. Nests were located by gently lifting intertidal rocks to expose an excavated nesting cavity, a guarder male and a brood of young beneath the rock (Fig. 1). We measured the guarding male fish located in these nests for standard length (to the nearest 1 mm) and body mass (to the nearest 0.1 g). Average (\pm SD) guarder male standard length was 20.9 ± 3.4 cm and body mass was 139.2 ± 69.9 g. We then digitally photographed their broods and later counted the young from the images using the software ImageJ (v.1.45; ImageJ, National Institutes of Health, Bethesda, MD, U.S.A., <http://rsbweb>.

nih.gov/ij/). Average (\pm SD) brood size was 561 ± 461 young. We calculated male body condition using the residuals from a regression of $\ln(\text{total body mass})$ against $\ln(\text{standard length})$.

We euthanized the males using an overdose of benzocaine (>250 mg/litre for 3 min) followed by cervical severance. Males were euthanized quickly and were promptly dissected to inspect their stomach contents and quantify the number of young consumed. We also removed and preserved in ethanol a small ($\sim 5 \times 5$ mm) clip from each male's caudal fin for paternity analyses. A previous study quantified digestive tract evacuation rates and showed that young remain semi-intact for about 24 h post-consumption before being fully digested within the digestive tract (Bose et al., 2015). Counts of consumed young were not possible via gastric lavage techniques and all of the euthanized males were used in a number of other studies (Bose et al., 2014, 2015; Cogliati, Balshine et al., 2014; Cogliati et al., 2013, 2015; Cogliati, Mistakidis et al., 2014). We also sampled ~40 young from every developmentally distinct cohort in the nest and preserved them in ethanol.

Paternity Analyses

We selected 33 guarder males and their young for detailed genetic paternity testing (see Table 1). For each of these guarder males, we identified the developmental stages of young from each cohort within their nest and also determined the stage of the young that each guarder male had consumed, if any. It is possible to classify plainfin midshipman young into one of nine distinct developmental stages based on the formation of key embryonic developmental features (Balon, 1999), and these developmental thresholds can be used to estimate age (see Cogliati et al., 2013 for

Table 1

Sample sizes of *Porichthys notatus* guarder males, by year and field site, used in this study

	2010	2011	2013	2015
Crescent Beach	6	12 (1)	121 (1)	0
Deep Bay	0	0	11 (4)	0
Ladysmith Inlet	16 (1)	20 (6)	66 (3)	45 (10)
Mill Bay	18 (3)	0	0	0
Nanoose Bay	0	0	21 (1)	3 (3)
Tomales Bay	0	8	0	0

Numbers in parentheses indicate the subset of males ($N = 33$ of 347) specifically selected for genetic paternity analyses, based on their digestive tract contents, to represent a wide range of young consumed (range 0–52 young/digestive tract) and to constitute a representative sample of guarder males in the wild in terms of body size and brood size ranges. These particular males were also chosen because they all had young in their nests that were at least 2 weeks old, ensuring that there would be a sufficient amount of embryonic tissue and paternal DNA for extraction (M. J. Lau & K. M. Cogliati, personal observations).

details). These 33 selected males were caring for an average (\pm SD) of 1.5 ± 0.6 developmentally distinct cohorts of young (range 1–3). Using a standard extraction protocol, we extracted DNA from the fin clips of these 33 males as well as the DNA from 5 to 35 young per cohort (for a total of 677 young from 50 different cohorts; see [Cogliati et al., 2013](#) for details). We also extracted DNA from the young found within the males' digestive tracts, although we did this only for the relatively intact and undigested young (for a total of 89 consumed young from 17 cannibalistic males). Then, we genotyped all adults and young at five polymorphic microsatellite loci (*Pon32*, *Pon47*, *Pon22*, *Pon23* and *Pon30*; see [Suk, Neff, Fitzpatrick, & Balshine, 2009](#) for more details on loci including levels of polymorphism and compliance with Hardy–Weinberg expectations). We carried out PCR amplification using a T1 thermocycler (Montreal Biotech Industries, Dorval, PQ, Canada), followed by fragment analysis at the NAPS unit in the University of British Columbia. Microsatellite alleles for each locus were scored for each individual based on characteristic peaks. We used the two-sex paternity model developed by [Neff, Repka, and Gross \(2000a, 2000b\)](#) and [Neff, \(2001\)](#) to estimate each male's paternity in each of his cohorts and to the group of young consumed. We then calculated average nest paternity using a weighted average across all cohorts in the nests depending on how many young were in each cohort. The two-sex paternity model also calculates the proportion of offspring per brood that is expected to be compatible with the putative father based on chance alone (NG_{dad}). These values can be used to yield the probability of excluding a random male from the population as the nest-guarding father (given by $1 - NG_{dad}$). NG_{dad} values for the broods in our study were on average (\pm SD) 0.23 ± 0.15 (range 0.01–0.49).

Note that paternity estimates from the young found in the digestive tracts of 11 out of these 33 guarder males have been published descriptively in [Cogliati et al. \(2015\)](#). Here, however, we expand upon those previously published results by incorporating them into a broader analysis of what factors underlie such cannibalism.

Ethical Note

Plainfin midshipman fish are common in many rocky intertidal zones across the west coast of North America; they are not considered threatened or endangered ([Collette, Acero, Betancur, Cotto, & Rojas, 2010](#)). All animals were handled only by highly trained personnel and fish were removed from the nest by wrapping them in damp towels to reduce light exposure, chances of desiccation and stress prior to euthanasia. The fish were moved to the chemical bath rapidly and efficiently (30–60 s per fish). We euthanized the fish using an overdose of benzocaine (>250 mg/litre for 3 min) followed by cervical severance. For any fish that were not euthanized, benzocaine was not used to anaesthetize them prior to their fin clipping. This is because fin clipping is a very quick procedure (<10 s) and removes a very small piece of tissue relative to the size of the whole caudal fin. Conversely, anaesthesia (and subsequent recovery) using a chemical bath takes a much longer time frame per fish (several minutes). After the fin-clipping procedure, the fish were immediately returned to their nests. This work was done in accordance with Canadian Department of Fisheries and Oceans (XR 50 2010, XR 126 2011, XR 14 2013, XR 81 2015) and California scientific collections permits (SC-0001380). The procedures used in this study were approved by the McMaster University Animal Research Ethics Board (AUP numbers 06-10-61, 10-11-70 and 13-12-52) and are in line with the guidelines set by the Canadian Council on Animal Care (CCAC) and [ASAB/ABS \(2018\)](#) regarding the treatment of animals in research and teaching.

Statistical Analyses

All analyses were conducted in R (v.3.5.1, [R Development Core Team, 2016](#)). We first investigated whether the observed degree of cannibalism of young (i.e. the number of young found in the digestive tract of each guarder male) was related to male body condition or his brood size. To do this, we fitted a generalized linear model specifying a negative binomial error distribution to account for overdispersion (GLM, MASS package; [Venables & Ripley, 2002](#)) to the larger data set of 347 guarder males. We included the

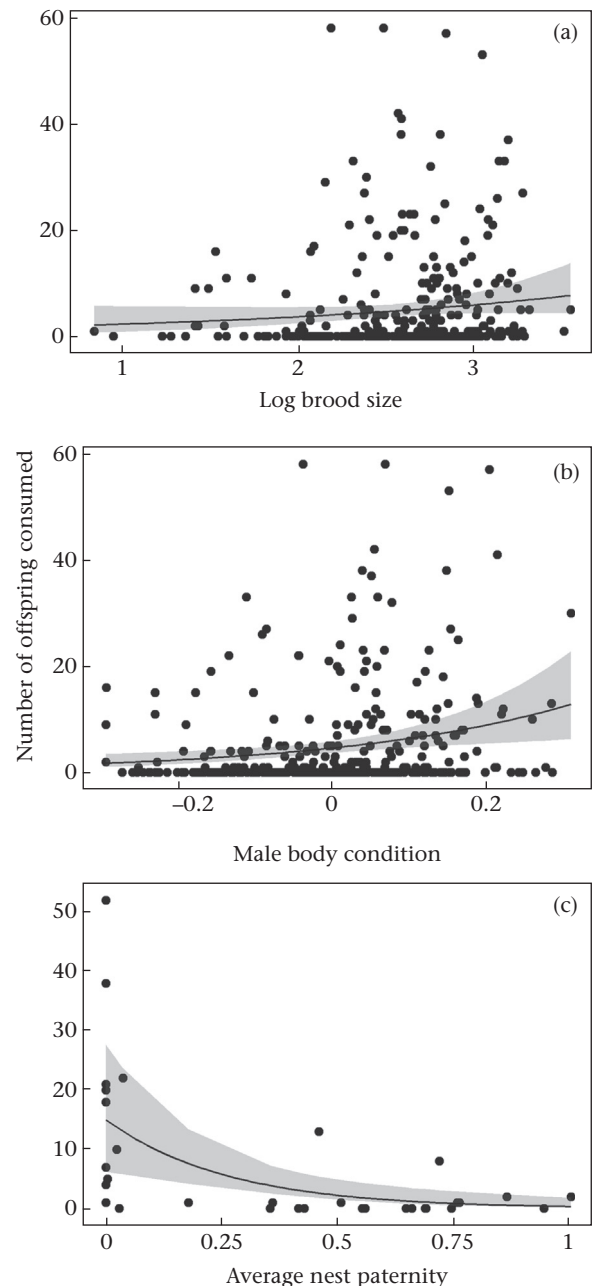


Figure 2. The number of young found within the digestive tracts of guarder male plainfin midshipman, *Porichthys notatus*, in relation to (a) male body condition, (b) brood size and (c) nest paternity. Note that panels (a) and (b) depict data from the larger data set ($N = 347$ guarder males), while panel (c) depicts data from the smaller, genotyped data set ($N = 33$). Plots show fits from negative binomial models with single predictor variables. Grey ribbons indicate 95% confidence intervals.

number of young consumed per male (count) as the response variable, and male body condition and brood size (log-transformed) as continuous predictor variables. Male standard length and the specific date of sampling (i.e. Julian date) were included as continuous covariates along with year as a categorical variable. All continuous variables were first scaled by dividing by their respective standard deviations and mean centred. Site was not included in the model, because a likelihood ratio test suggested that it did not significantly improve model fit (LRT = 10.25, $df = 5$, $P = 0.07$). Furthermore, including site as a random intercept did not account for any additional variation (marginal $R^2 = 0.104$; conditional $R^2 = 0.104$; trigamma estimates, MuMIn package, Barton, 2018).

Next, we investigated whether the number of young consumed by each male could be explained by his average paternity within his nest. We used the GLM model above (fitted to our large data set) as a guide for analysing our smaller, paternity-focused data set. Specifically, we fitted the same model as above and included average nest paternity as a new predictor variable, but we removed male standard length because it did not correlate with partial brood cannibalism in our large model.

Finally, we examined whether cannibalistic males preferentially consumed nonkin young from within their nests, and we did this in two different ways. First, we asked whether the cannibalistic males' paternity estimates to the young in their digestive tracts were lower than the paternity estimates to the young in their nests. To do this, we used a paired t test on the paternity estimates of the consumed young versus the remaining young in the nest. Second, we asked whether males had cannibalized young from one of their cohorts preferentially and, if so, whether they specifically targeted the cohort with the lowest paternity. We did this by using a one-sample Wilcoxon signed-rank test on the difference values between the paternity of the cannibalized cohort and the average paternity of the remaining cohorts.

RESULTS

Based on our observations from 347 nests, we found that males consumed on average (\pm SD) 5.0 ± 9.9 young, and that the number of young consumed ranged from 0 to 58. The number of young found in male digestive tracts decreased as the breeding season progressed (GLM: estimate \pm SE = -1.13 ± 0.14 , $z = -8.05$, $P < 0.0001$). Males in better body condition consumed more young (estimate \pm SE = 0.48 ± 0.12 , $z = 4.03$, $P < 0.0001$; Fig. 2a). Neither brood size ($P = 0.28$; Fig. 2b) nor male standard length ($P = 0.21$) were related to the number of young consumed, although the degree of partial brood cannibalism varied significantly across years ($\chi^2_3 = 51.3$, $P < 0.0001$).

Based on our smaller data set of genotyped nests ($N = 33$), we found that males varied in their paternity to the broods under their care, ranging from 0 to 100%, with an average (\pm SD) paternity estimate of $37 \pm 34\%$. Some of these males had sired offspring in their nests, while others had likely taken over their nest from a previous male resident. We identified 13 clear cases of nest take-overs because the males had average brood paternity estimates of $0.7 \pm 1.3\%$ (range 0–3.6%). The remaining 20 males had average brood paternity estimates of $60.8 \pm 20.9\%$ (range 17.7–100%). The genotyped males consumed on average 6.9 ± 12.0 young (range 0–52), and the number of consumed young increased significantly as average brood paternity decreased (GLM: estimate \pm SE = -3.06 ± 1.04 , $z = -2.94$, $P = 0.003$; Fig. 2c). The 13 take-over males consumed 15.3 ± 15.7 young (range 0–52), while the remaining 20 non-take-over males consumed 1.5 ± 3.3 young (range 0–13). In this smaller data set ($N = 33$), the number of young cannibalized did not vary with male body condition

(estimate \pm SE = 0.28 ± 0.28 , $z = 1.01$, $P = 0.31$) or brood size (estimate \pm SE = 0.07 ± 0.34 , $z = 0.21$, $P = 0.83$).

Twenty-one out of the 33 genotyped males had cannibalized some young. For 17 of these 21 males, we estimated the paternity to the young in their digestive tracts to be $9.3 \pm 11\%$ (average \pm SD; range 0–36%), which was lower than their paternity estimates to the broods in their nests (average \pm SD = $37 \pm 34\%$, range 0–100%), but this difference did not reach statistical significance (t test: $t_{16} = -1.90$, $P = 0.076$). Next, to test whether males preferentially cannibalized from the cohort(s) in their nests with the lowest paternity scores, we focused on a subset of our genotyped males. This subset consisted of males that (1) had cannibalized young, (2) had sired offspring in their nests (i.e. were not take-over males) and (3) had more than one cohort of young under their care. Only five out of the 33 males met all of these criteria. The developmental stage of the consumed young always matched the developmental stage of one cohort in the males' nests, suggesting that males indeed preferentially consumed from a single cohort within their respective nests. However, the males did not appear to specifically target the cohort with the lowest paternity estimate (Wilcoxon signed-rank test: $V = 5$, $P = 0.63$).

DISCUSSION

It is rare for the relationship between paternity and partial brood cannibalism to be studied in wild animal populations. The majority of past studies have involved laboratory manipulations, such as brood transplants or experimental exposures to cuckolders, followed by behavioural observations (e.g. Bandoli, 2002; Green, Mirza, & Pyle, 2008; Svensson & Kvarnemo, 2007; Vallon, Anthes, & Heubel, 2016). Our data show that wild plainfin midshipman guarder males engage in high levels of offspring cannibalism when their genetic relatedness to the brood is low or zero, which occurs after they take over a nest from a previous resident (here, nest take-overs can be used as a reliable indirect paternity cue; Sherman & Neff, 2003). This result provides support for the relatedness hypothesis. Even though cuckoldry also occurs in this system – from both sneaker and guarder males alike – cuckoldry tactics generally do not account for such large or absolute losses in paternity, whereas take-overs do (Cogliati, Balshine et al., 2014; Cogliati et al., 2013). We also show that males that had sired offspring in their nests (i.e. non-take-over males) still cannibalized young, although to a far lesser degree, and these males sometimes even consumed their own genetic offspring. Numerous nonmutually exclusive hypotheses exist for why parents sometimes cannibalize offspring under their care (Manica, 2002). Here, we tested the brood size hypothesis and the energy reserves hypothesis, finding no support for either, because males with large broods or in poor body condition did not consume more young.

Our results suggest that plainfin midshipman males act cannibalistically when confronted with nonkin young in the nests that they take over (see also Bose et al., 2016). Midshipman nests are considered to be strongly space limited (Bose et al., 2018; DeMartini, 1988, 1991), and so nonkin young take up valuable space that could otherwise be used for future cohorts with potentially higher paternities. Caregiving males with low or uncertain paternity are therefore faced with a trade-off – to cannibalize young and clear space for potentially more valuable offspring in the future, or to continue caring for the current young. In the case of nest take-overs, the solution to the trade-off appears to be to cannibalize young, as all the current young are unrelated to the new male. We could clearly identify some males as take-over males, because they had nest paternity estimates near or equal to 0% and these males had consumed large numbers of young (average \pm SD = 15.3 ± 15.7 young, range 0–52) at the time of

capture. In a large-scale field experiment, Bose et al. (2016) showed that fewer of the original young survive under the allocare of a take-over male compared to young that remained under the care of their actual father. In cases where males have sired offspring in their nests, the solution to the trade-off of whether or not to cannibalize is not as straightforward. Plainfin midshipman males appear unable to use direct offspring cues to distinguish individual kin from nonkin young (Bose et al., 2016) and so any males that cannibalize from nests where they have already mated and sired young risk committing filial cannibalism. Our results indicate that some consumed young are indeed related to their cannibal father, and therefore these males incurred some direct fitness costs by eating their own young. Males with own offspring in their nests only consumed an average of 1.5 ± 3.3 young (range 0–13), far fewer than take-over males did (average \pm SD = 15.3 ± 15.7 young, range 0–52). It is unclear whether these low levels of cannibalism serve to clear space for future cohorts, whether they occur as a form of parental care (e.g. to reduce offspring density or remove diseased offspring), or if they are a means to optimize parental investment (e.g. to remove low-quality or slow/late-developing offspring). Alternatively, low levels of cannibalism can occur by accident, incidental to nest cleaning. Interestingly, we observed low levels of cannibalism in nests ranging widely in their paternity estimates, including in nests with 100% paternity (see Fig. 2c). In our smaller, paternity-focused data set, once all cases of nest take-overs were omitted, no clear relationship was found between brood paternity and partial brood cannibalism (GLM: $N = 20$, estimate \pm SE = 0.17 ± 2.40 , $z = 0.073$, $P = 0.94$); however, the statistical power of this test was limited. Overall, it appears that partial brood cannibalism in the plainfin midshipman fish system can be divided into two categories: high levels of cannibalism associated with nonpaternity and driven by nest take-overs versus low levels of cannibalism that may be driven by other factors.

We did not find that midshipman males in charge of mixed-paternity broods selectively consumed unrelated young or that they preferentially cannibalized from the cohort with the lowest paternity, and this may be because males lack the ability to differentiate kin from nonkin in their nest. Assessing paternity and distinguishing own young from nonkin young generally occurs through the use of either direct (phenotypic) or indirect (social/environmental) cues of relatedness (Sherman & Neff, 2003). Males of several species have been shown to respond to direct cues of compromised paternity by reducing their parental activities and/or increasing their rates of offspring cannibalism (bluegill sunfish, *L. macrochirus*: Neff, 2003; flour beetles, *Tribolium confusum*: Parsons, Zhong, & Rudolf, 2013; mangrove rivulus, *Kryptolebias marmoratus*: Wells & Wright, 2017; poison frogs, *Allobates femoralis*: Ringler, Beck, Weinlein, Huber, & Ringler, 2017). However, a previous transplant experiment showed that midshipman males do not adjust care when their broods have been exchanged with foreign young, suggesting that they may not be able to recognize direct offspring cues (Bose et al., 2016). Further research in plainfin midshipman is now warranted to test how indirect cues may influence males' tendencies to cannibalize while also controlling for additional variables such as age and quality of the young.

Interestingly, males that took over a nest did not typically cannibalize the entire brood that they acquired and even continued to care for some of them. Bose et al. (2016) showed that even a month after a take-over event, a nest can still retain some of the original nonkin young under the care of the alloparent. Retaining at least some nonkin young may confer a fitness benefit to a take-over male, perhaps in terms of future mate attraction or offspring dilution effects (Jamieson, 1995; Lindström, St Mary, & Pampoulie, 2006; Matsumoto & Takegaki, 2013; Wisenden, 1999). Sargent (1989) described an analogous situation in the fathead minnow,

P. promelas, in which alloparental males reduce their adopted broods down to a size that still attracts females to their nests, but permits enough nest space for the new eggs to be laid. These possible benefits still require explicit testing in plainfin midshipman fish.

We found that the number of young in male digestive tracts decreased across the breeding season and that males in better body condition consumed more young. These results suggest that energetic demands are not related to cannibalism of young in plainfin midshipman fish (Bose et al., 2014, 2015). The males that consumed the most young had some of the highest body condition scores, most likely because these were successful nest usurpers that had spent relatively less time providing costly parental care depleting their energy stores (Bose et al., 2015). Nest take-overs also occur more frequently early in the breeding season (Bose et al., 2014; Cogliati et al., 2013), explaining the observed decline in cannibalism as the season progresses. In our study, brood size did not influence brood cannibalism. Theory suggests that partial brood cannibalism should be more prevalent in larger broods because the costs of losing offspring are proportionally smaller for these large broods (Manica, 2002; Sargent, 1992). A number of previous studies have also failed to detect a correlation between brood size and the degree of partial brood cannibalism by caregivers (e.g. fathead minnows, *P. promelas*: Sargent, 1988; scissortail sergeant, *A. sexfasciatus*: Manica, 2003, 2004; maritime earwig, *A. maritima*: Miller & Zink, 2012; Lusitanian toadfish, *Halobatrachus didactylus*: Felix et al., 2016). Broods that become too small may simply be completely cannibalized rather than only partially so.

We did not detect any clear differences in partial brood cannibalism across our field sites. Since we implicate nest take-overs as a major driver of partial brood cannibalism in *P. notatus*, this may suggest that rates of nest take-overs are also similar across sites. These results mirror those of Cogliati, Mistakidis et al. (2014), who reported remarkable similarity in ecological factors across plainfin midshipman populations: nest site availability, paternity patterns and metrics of sexual selection were highly similar across numerous midshipman breeding beaches.

While numerous hypotheses exist for why parents sometimes cannibalize the young under their care, no single hypothesis has been able to explain the occurrence of cannibalism across all taxa (Manica, 2002). The energy reserves hypothesis has received the most experimental investigation and support across taxa in the past, and the brood size hypothesis also is well grounded in theory (Manica, 2002), yet neither of these hypotheses appear to explain cannibalism in the plainfin midshipman fish. Rather, the relatedness hypothesis explains a large amount of the variation in partial brood cannibalism in this species. High levels of cannibalism in the plainfin midshipman are associated with nonpaternity and driven by nest take-overs, while low levels of cannibalism appear to be driven by other factors. We suggest that take-over males may use cannibalism to clear valuable space for their own future offspring within the cramped confines of their intertidal nests. Our findings are also in line with theory, as individuals are expected to reduce parental investment and cannibalize more when faced with reliable cues of low parentage (Owens, 1993; Westneat & Sherman, 1993). Few studies to date have studied offspring cannibalism by concurrently testing more than one hypothesis at a time and we emphasize how using such a multipronged approach can lead to a more comprehensive understanding of the factors that underlie this seemingly paradoxical behaviour.

DECLARATIONS OF INTEREST

We have no declarations of interest.

Acknowledgments

We thank Mr Warren Johnny and the Stz'uminus First Nation as well as Pamela Walker, Ross Shepard, Captain Bill and Rubie Cogswell, Eileen Carr and family for providing access to field sites. We thank Shawn Garner for his help with paternity data. We thank Chuck and Sally Flader and Dvori and Michael Balshine for their hospitality. We also thank Ahdia Hassan, Julie Marentette, Celia Chui, Allison Mistakidis, Jen Reynolds, Holly Howe and Nick Luymes for their assistance collecting the field data. This work was funded by a Natural Sciences and Engineering Research Council of Canada grant to S.B. (grant no. 222854-2011). Additional funding was provided to A.P.H.B. from the PADI Foundation and to A.P.H.B. and K.M.C. from the McMaster University Graduate Students Association and the Department of Psychology, Neuroscience and Behaviour at McMaster University.

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